Syst. Biol. 50(2):290–300, 2001

Species or Supraspecific Taxa as Terminals in Cladistic Analysis? Groundplans Versus Exemplars Revisited

LORENZO PRENDINI

Percy FitzPatrick Institute, University of Cape Town, Rondebosch, 7701, South Africa;
E-mail: lprendin@botzoo.uct.ac.za

> "Perhaps the platonic mysticism of archetypes resonates in systematics today in intuitive groundplan analyses."
>
> (Yeates, 1995:347)

Increasing the number of taxa in a phylogenetic analysis can have a profound effect on accuracy (Hendy and Penny, 1989; Wheeler, 1992; Hillis, 1996; Graybeal, 1998; Halanych, 1998; Soltis et al., 1998; but see also Kim, 1996; Poe and Swofford, 1999). Although including all or most constituent species in analyses attempting to resolve relationships among higher taxa is desirable, it may be impractical (Donoghue, 1994; Mishler, 1994; Nixon and Carpenter, 1996; Rice et al., 1997). The number of possible cladistic arrangements increases exponentially with the addition of taxa (Felsenstein, 1978), thus requiring more complex analyses, which cannot guarantee optimal solutions or may be intractable with available computer technology.

Two alternative approaches for overcoming this constraint on the number of taxa included in an analysis differ in the use of species versus supraspecific taxa as terminal entities. Both have the same aim—to estimate the groundplan, or plesiomorphic states, of the higher taxa concerned. The choice between these approaches is intimately related to the problem of analyzing large data sets. As the number of large data sets has increased, so has the number of papers addressing this issue (e.g., Nixon and Davis, 1991; Donoghue, 1994; Mishler, 1994; Yeates, 1995; Nixon and Carpenter, 1996; Kron and Judd, 1997; Rice et al., 1997; Bininda-Emonds et al., 1998; Griswold et al., 1998; Wiens, 1998a). However, no apparent consensus has been reached, and empirical studies using either approach, or a combination thereof, continue to appear.

On the basis of comparisons of real and hypothetical data matrices, several authors have argued in support of species as terminal taxa (Yeates, 1995; Kron and Judd, 1997; Griswold et al., 1998; Wiens, 1998a). In a recent simulation study, Wiens (1998a:411) concluded that "using species as terminals gives consistently more accurate estimates than do the other coding methods, even when only a few species are sampled from each higher taxon[and is] strongly recommended for empirical studies." Other authors advocate the use of supraspecific terminal taxa (Rice et al., 1997; Bininda-Emonds et al., 1998). For example, Rice et al. (1997:560) rejected the use of species as terminals because "if we confine ourselves to choosing among terminal taxa, we will inevitably lengthen branches, with all the attendant problems" and proposed the inferred ancestral states (IAS) method for coding supraspecific terminals (see below) as a "more promising avenue." In the present contribution, I will argue from first principles that the use of species as terminals is superior, both practically and philosophically, to the use of supraspecific terminals. I will then provide criteria for selection of species, given the varying availability of data.

DEFINITIONS

As the literature on methods for coding and sampling higher taxa has diversified, so has the terminology. The traditional approach to the analysis of higher-level phylogenetic relationships using higher taxa as terminals (Wiens, 1998a) has been variously referred to as groundplan analysis (Yeates, 1995; Griswold et al., 1998), summary terminals (Nixon and Carpenter, 1996), and supraspecific terminal taxa (Bininda-Emonds et al., 1998), whereas the use of species as terminals (Kron and Judd, 1997; Wiens, 1998a) is commonly referred to as the exemplar approach (Mishler, 1994; Yeates, 1995; Bininda-Emonds et al., 1998; Griswold et al., 1998). Insofar as both approaches aim to estimate the ancestral groundplan, the term *groundplan* is misleading when used as a synonym for *supraspecific terminal* (e.g., Yeates, 1995). The term *exemplar* is equally misleading when referring to supraspecific terminals (e.g., Smith, 1996), because of its historical precedence in studies using species as terminals and because it may also apply to individual specimens (see below). In view of this confusion, a brief elaboration of the methods, and corresponding terms, is provided in the following section.

Supraspecific Terminal Taxa

The traditional morphological approach to the analysis of higher-level relationships involves estimating the plesiomorphic states of the higher taxa under consideration, from observations of a sample of their constituent species (or the extraction of character state information from the literature), and then summarizing this character state information into supraspecific terminals. This approach is exemplified in such studies as those by Raven (1985), Shultz (1990), Brothers and Carpenter (1993), Goloboff (1993), Hausdorf (1995), Morrone (1997), and Rognes (1997).

Yeates (1995) considered this approach to groundplan estimation to be intuitive, there being no detailed description of the method. In fact, this approach proceeds by a variety of methods that are seldom specified. Bininda-Emonds et al. (1998:105) provided a formalization of the methods in an effort to "make . . . the method more rigorous." According to those authors, groundplan estimation may be conducted by means of (1) the ancestral method, in which fossil or ontogenetic evidence is used (e.g., Bryant et al., 1993), or a hypothetical ancestor (archetype) reconstructed on the basis of previous phylogenetic analysis (compartmentalization [Mishler, 1994] and related methods; e.g., Donoghue and Doyle, 1989); or (2) the democratic method, in which character states are scored according to what amounts to the "common equals primitive" criterion, by consensus in character states among a sample of species, much as species traits are delimited from a sample of specimens (e.g., Bininda-Emonds and Russell, 1996).

Wiens (1998a) recognized the distinction between the democratic method of Bininda-Emonds et al. (1998) (his majority method)—in which variable higher taxa are coded according to the modal condition among the species (e.g., Livezey, 1986) or according to a consensus (e.g., Trueb and Cloutier, 1991)—and methods for inferring ancestral or primitive states. However, unlike Bininda-Emonds et al. (1998), Wiens (1998a) further recognized the distinction between methods for inferring *primitive* states, which involve coding the supraspecific taxon with plesiomorphic states determined in previous higher-level analyses of relationships among the outgroups, and those for inferring ancestral states, in which the supraspecific taxon is coded with plesiomorphic states determined in previous lower-level analyses of internal relationships within the supraspecific taxon.

These latter methods for inferring ancestral states, which include the placeholder approach (Donoghue, 1994), compartmentalization (Mishler, 1994), and IAS (Rice et al., 1997), were listed under the ancestral method by Bininda-Emonds et al. (1998). They differ from, and are more defensible than, other methods for coding supraspecific terminals (including methods for inferring primitive states). They are explicit and quantitative, rather than intuitive, because they involve optimization of characters onto a cladogram, instead of relying on a priori assessments of character polarity. Beyond these advantages, such methods are subject to the principal criticisms directed toward supraspecific terminal taxa, as outlined below (refer also to Meacham, 1984, 1986; Colless, 1985; Clark and Curran, 1986; Nixon and Carpenter, 1996; Wiens, 1998a).

Exemplars, Species, and Individuals

The exemplar approach differs fundamentally from the various methods for coding supraspecific terminal taxa because it involves selection of a sample of species from each higher taxon, which are then scored as separate terminals. This approach is exemplified in such studies as those by Christofferson (1989), Grimaldi (1990), Miller (1991), Yeates (1994), Judd (1996), Rosell and Uriz (1997), and Griswold et al. (1998).

What constitutes an exemplar species differs between analyses based on molecular data and those based on morphology. Individuals usually constitute the terminal taxa in analyses that are based on molecular data (Vrana and Wheeler, 1992; Kron and Judd, 1997). These individuals may then be viewed as exemplars for species they represent. Morphological data, although similarly gathered from individual specimens, are usually summarized as diagnosable populations, or species, which then become terminal taxa (Frost and Kluge, 1994). The main reason for this difference is the operational treatment of morphological data in taxa with distinct semaphoronts (e.g., comparable sexes, life stages). Morphological observations from individual semaphoronts of each sex or life stage (e.g., larva, pupa or adult) are often combined into a single terminal to avoid missing entries that would result from treating the individual semaphoronts as separate terminal taxa.

OBJECTIONS TO SUPRASPECIFIC TERMINALS

Yeates (1995) provided a cogent argument in support of exemplars as terminal taxa. As elaborated by Yeates (1995), Kron and Judd (1997), Griswold et al. (1998), and Wiens (1998a), numerous practical and philosophical reasons favor the use of exemplar species rather than supraspecific terminal taxa for phylogenetic analysis. The following section shall serve to reinforce those reasons.

Repeatability

From a practical perspective, the exemplar approach is preferable because the methods are explicit and repeatable—the use of exemplars necessitates articulation of the criteria invoked for exemplar selection. Any application of the exemplar approach may be criticized on the basis of the exemplars chosen, but disagreements can be resolved by including all suggested terminals in a simultaneous analysis (Yeates, 1995). In contrast, the covert nature of many assumptions required in the formulation of supraspecific terminals (excepting quantitative methods for inferring ancestral states) is not conducive to collaboration between workers who are relying on different assumptions of terminal group structure, character transformation, character distribution, or a combination thereof, and may hinder future analyses by preventing the addition of new taxa or character states.

Simultaneous Analysis

In addition to the strong potential for repeatability, the exemplar approach is superior for simultaneous analysis (total evidence sensu Kluge, 1989) of morphological and molecular data (Kron and Judd, 1997). Except for recent IAS analyses of the *rbc*L dataset (Rice et al., 1997), the use of supraspecific terminal taxa has been virtually restricted to morphological analyses, whereas the use of exemplars is de rigueur for molecular studies (Yeates, 1995; Bininda-Emonds et al., 1998).

In supporting their argument for supraspecific terminal taxa, Bininda-Emonds et al. (1998:128) stated that the "literature contains numerous molecular studies that include results that most would consider incorrect . . . our results suggest that the use of the exemplar method . . . might be causing errors in analyses." In view of widespread indications that increased taxonomic sampling improves the accuracy of phylogenetic analyses (Hendy and Penny, 1989; Wheeler, 1992; Hillis, 1996; Graybeal, 1998; Halanych, 1998; Soltis et al., 1998; but see also Kim, 1996; Poe and Swofford, 1999), the "incorrect" results noted by Bininda-Emonds et al. (1998) can probably be attributed to inadequate sampling, rather than to use of the exemplar method per se. Many molecular phylogenetic studies sample only a single exemplar species from each higher taxon, which has been shown to yield low accuracy under many conditions (Wheeler, 1992; Wiens, 1998a). Nonetheless, more accurate estimates are consistently obtained by using the exemplar approach even when only a few additional species are sampled per higher taxon (Wiens, 1998a).

Bininda-Emonds et al. (1998) refrained from suggesting an alternative to the exemplar approach that would be more effective for analysis of molecular data. IAS (Rice et al., 1997) might provide such an alternative. However, the efficacy of IAS will always depend on the quality of the a priori estimated phylogenies and the ancestral state reconstructions within the higher taxa (Wiens, 1998a).

Assumptions of Monophyly

In common with all methods using supraspecific terminals the principal philosophical objection to IAS is the assumption of monophyletic supraspecific taxa (Yeates, 1995;

Kron and Judd, 1997; Bininda-Emonds et al., 1998). The exemplar approach is superior in this regard, because the terminal taxa, species, are defined on criteria of diagnosability, rather than monophyly (Nelson and Platnick, 1981; Cracraft, 1983, 1989; Nixon and Wheeler, 1990; Wheeler and Nixon, 1990; Davis and Nixon, 1992). This should not be taken to imply that the assumption of monophyly does not also apply at the species level, only that it becomes increasingly difficult to defend this assumption with progressively more inclusive taxa (genera, families, orders, and so forth). A further philosophical advantage of using exemplars is the potential for testing the monophyly of higher taxa in analyses by representing each with more than one exemplar species (Nixon and Davis, 1991)—an important consideration if testing the monophyly of taxa as well as the relationships among them are seen as equally important goals of phylogenetic analysis.

Assumptions of Character Polarity

Aside from testing the monophyly of higher taxa, a major strength of using exemplar species is the potential to resolve relationships within each higher taxon (in the course of a global analysis) and thereby better resolve the ancestral states of the higher taxa (Wiens, 1998a).

The exemplar approach is preferable for interpreting character polarity because it makes use of observable and verifiable data, rather than hypothetical states and character combinations (Griswold et al., 1998). Most importantly, no untested decisions are made a priori regarding the polarity of character states scored in the terminal taxa.

As noted above, methods for inferring ancestral states (IAS, compartmentalization, and so forth) differ from other intuitive methods in this regard. When the former methods are applied, decisions regarding polarity do not go untested a priori: Indeed, the lower-level cladogram on which they are optimized is a test. However, the decisions cannot be tested again in global analyses that use supraspecific terminals.

Coding Interspecific Variation

Assessment of character polarity within supraspecific taxa may be particularly difficult for analyses with rampant interspecific variation (especially prevalent at lower taxonomic levels) and may render assignment of plesiomorphic states intractable for groundplan estimation. Interspecific variation may require that supraspecific terminals be scored as polymorphic or missing for variable character states (Rice et al., 1997), or may even result in omission of characters that could readily be included in analyses with exemplar species (Kron and Judd, 1997). Wiens (1998a) referred to these practices as the polymorphic/missing and fixed only methods, respectively, for dealing with interspecific variation and noted that variability within higher taxa is one of the most common criteria for excluding characters.

The main disadvantage of coding variable states as missing or polymorphic is that they become essentially uninformative (Wiens, 1998a). In addition, coding variable higher taxa as missing can produce trees that are inconsistent with those based on scoring species as terminals (Nixon and Davis, 1991). Furthermore, the practice of discarding variable characters is unacceptable because it ignores potentially informative data (de Queiroz, 1987; Estes et al., 1988) and thus lowers accuracy (Wiens, 1998a).

These problems do not arise if exemplar species are used. When exemplars display interspecific variation for a particular character, several possible states may be assigned to the supraspecific groundplan (i.e., the state assignment will be equivocal), reflecting the fact that the parsimony criterion alone cannot always distinguish a single state in a hypothetical ancestor (Yeates, 1995). Conflicts over groundplan states may be resolved by adding more exemplars, an option that is unavailable if supraspecific terminals are used.

Extrapolation

Although supraspecific terminal taxa are not usually applied in molecular studies, extrapolation (Sensu Nixon and Carpenter, 1996) of the presumed plesiomorphic condition in morphological characters to the exemplars chosen for molecular sampling is commonplace in simultaneous analyses. Examples of this practice may be found in Eernisse and Kluge (1993), Dragoo and Honeycutt (1997), Whiting et al. (1997), Nandi et al. (1998), Wheeler and Hayashi (1998), and Wiley et al. (1998). Scoring morphological character states for the specific exemplar species used in the analysis (e.g., Miller et al., 1997; Shaffer et al., 1997) is comparatively rare.

Extrapolation of morphological characters may be justifiable for groups that are well-known (e.g., vertebrates, chelicerates, and holometabolous insects) and may be a necessity for anatomical, embryological, or secondary chemical characters known from relatively few samples of species (e.g., endothermy in vertebrates, double fertilization in angiosperms, holometaboly in insects, rather than omitting these characters from the analysis (Nixon and Carpenter, 1996)). Nevertheless, for the majority of morphological characters, especially in less well known groups and at lower taxonomic levels, extrapolation cannot be justified without the risk of biasing the outcome towards an expected result.

Hypothetical Ancestors and Rooting

Many cladistic analyses incorporate an a priori hypothetical ancestor, included in the data matrix as an additional terminal taxon and used to root the resulting tree (e.g., Nielsen and Kristensen, 1996; Marvaldi, 1997; Bogdanowicz et al., 1998). The use of hypothetical ancestors for rooting trees in phylogenetic analysis is directly related to this discussion because hypothetical ancestors are nothing more than supraspecific terminal taxa.

Bryant (1997) recently provided an empirical comparison of methods for producing hypothetical ancestors and distinguished between hypothetical ancestors inferred by outgroup comparison and those inferred with the ontogenetic and paleontological methods (see also Meier, 1997). These approaches to coding hypothetical ancestors are epistemologically equivalent to the methods for inferring primitive versus ancestral states, respectively, for supraspecific terminal taxa (discussed above). Because the former approach is based on outgroup analysis, inferences regarding plesiomorphic character states apply to the outgroup node; in contrast, the latter approach is based on the internal phylogeny of the supraspecific terminal taxon (i.e., ingroup), and inferences regarding plesiomorphic character states apply to the ingroup node (Bryant, 1997; Wiens, 1998a).

Whereas use of a hypothetical ancestor is necessary in rooting when using the ontogenetic and paleontological methods, inferences regarding character polarity based on outgroup comparison should not be summarized as hypothetical ancestor (Bryant, 1997). Inclusion of hypothetical ancestors inferred through outgroup comparison relies on a priori assumptions of character polarity and can produce results different from those obtained in analyses in which actual outgroup taxa are included (Nixon and Carpenter, 1993). Nonetheless, some authors continue to argue in support of hypothetical ancestors for summarizing inferences from many potential outgroups when appropriate outgroups have not been identified (e.g., Beard, 1993; Polly, 1996). Those authors argue that using hypothetical ancestors avoids digressions regarding outgroup relationships and thereby allows analyses of larger ingroups without resorting to inexact heuristic searches (Livezey, 1996). In practice, the inclusion of specific outgroups is rarely a problem with modern hardware and recent computer algorithms, whereas the assumptions associated with use of a hypothetical ancestor seldom justify substitution of the actual outgroups (Nixon and Carpenter, 1993; Bryant, 1997).

Practical Difficulties, Extra Effort, and Historical Inertia

Despite evident drawbacks, the use of supraspecific terminals persists, particularly in morphological studies of higher-level relationships, where it hinders the integration of morphological and molecular data matrices (particularly at lower taxonomic levels), beyond extrapolation in well-known groups. One possible reason for continued use of supraspecific terminals could be the practical difficulties of obtaining certain taxa (especially types) for examination. This may have encouraged the widespread practice of extrapolating morphological data directly from the taxonomic literature without verification in the actual specimens (e.g., Dragoo and Honeycutt, 1997; Wiley et al., 1998; Zrzavý et al., 1998). Besides perpetuating errors, such extrapolation may necessitate a democratic or common equals primitive assessment for state assignment in many characters (if these are not omitted or coded as polymorphic or missing). Although the common equals primitive assumption may have some predictive value within variable taxa, at least at low and intermediate rates of character change (Wiens, 1998a), this practice should be avoided.

Another possible reason for the persistent use of supraspecific terminal taxa may be the extra effort required to score exemplars for morphological analysis. Extra effort may be involved in examining species for which character states differ from the putative groundplan states for the higher taxon, as reflected in the literature. Furthermore, resolving species relationships within higher taxa may require extra effort to score additional characters that would be uninformative if supraspecific terminals were used (Wiens, 1998a).

On the other hand, perhaps the continued use of supraspecific terminals is merely another of the "many common practices of morphological phylogenetics [that] seem to owe their widespread use to historical inertia rather than quantitative investigation" (Wiens, 1998b:442). The use of supraspecific terminals (including hypothetical ancestors for rooting) may be a relic from the days when manual construction of cladograms was prevalent, and analysis of datasets with many terminal taxa was computationally impossible. In their discussion of hypothetical ancestors, Nixon and Carpenter (1993) considered the view that polarity had to be determined before cladistic analysis as a holdover from the use of algorithms that required construction of prerooted trees. Such programs, together with manual cladogram construction, required prior inference of an ancestor that represented hypotheses regarding plesiomorphic states for the ingroup. This practice continued even when prerooted trees were no longer necessary, as a means of enhancing the efficiency of older parsimony algorithms run on less powerful computers (Bryant, 1997).

CRITERIA FOR EXEMPLAR SELECTION

A commonly expressed reason for using supraspecific terminal taxa in favor of exemplars is the philosophical question of exemplar choice (Yeates, 1995; Bininda-Emonds et al., 1998). The exemplar approach requires the selection of a few species from the broader set of possibilities (assuming it is still computationally impossible to include all the species within a large monophyletic group), thus raising the issue of what criteria should be used for their selection. As is widely recognized, exemplar selection may seriously affect the outcome of phylogenetic analyses, because the derived character states of many extant species reduce the utility of these species as accurate estimators of the groundplans of their higher taxa (Donoghue et al., 1989; Lecointre et al., 1993; Adachi and Hasegawa, 1994; Doyle et al., 1994). However, the selection of exemplar species scarcely differs epistemologically from the estimation of plesiomorphic states for a supraspecific terminal taxon: The choice has merely shifted from the character states to the species that possess them. In the following section, I provide criteria for selection of exemplars, given the varying availability of data.

Basal Exemplars

Yeates (1995) and Griswold et al. (1998) advocate selecting exemplars, the character combinations of which most closely resemble the groundplans of their higher taxa, as reconstructed by previous phylogenetic analyses at a lower level. According to those authors, the most basal taxa, or representatives of the most basal lineages, should be selected as exemplars. Derived species, the character combinations of which differ markedly from the putative plesiomorphic condition of their higher taxa, should be ignored on the grounds that such variation is "irrelevant to the problem" (Griswold et al., 1998:4).

Two considerations are paramount with respect to the selection of basal exemplars. First, rather than simply selecting species that occupy basal positions in a phylogenetic hypothesis of a terminal group, species should be selected that exhibit the greatest number of plesiomorphic states. In morphological studies, especially where rooting is by hypothetical ancestor, these will often be the most basal species; in molecular studies, however, basal branches may be very long, and somewhat more distal species may exhibit shorter branches (patristic distance) from the root node. Second, when more than one exemplar is selected from a terminal group for which a phylogenetic hypothesis is available, each branch that arises from the basal node of the terminal group should be represented. These two criteria can and should be used in tandem. In short, when a phylogenetic hypothesis is available for the terminal group in question, an exemplar species with a short branch length should be selected from each of the two branches arising from the root node.

Maximally Diverse Exemplars

Selection of basal exemplars may be philosophically superior when hypotheses of relationships within terminal groups are available but will be inapplicable to the many cases for which such hypotheses are absent. In these cases, a choice must be made between random and maximal diversity approaches to exemplar selection. Random exemplar selection may be preferred for obtaining an "unbiased" sample. However, if the maximal diversity criterion used for exemplar selection is designed to test hypotheses of hierarchical structure, that would be more concordant with the hypothetico-deductive principles espoused by many cladists (e.g., Farris, 1983; Kluge, 1997).

Rather than adopt a random approach in circumstances where cladograms of lower-level relationships are unavailable, I argue for a maximal diversity approach to exemplar choice. The theoretical justification for this approach is based on Popperian testability: Exemplars should be chosen so as to provide the strongest test of monophyly for the higher-level taxa they represent. This is achieved by maximizing the chances of discovering homoplasy (Griswold et al., 1998) rather than by ignoring whatever variation may differ from the presumed plesiomorphic condition.

In practice, at least two exemplars should be chosen to reflect maximal diversity within the terminal group. A priori assessment of maximal diversity will usually reflect morphological variation (which in molecular studies is often assumed to reflect genetic variation) and may be equated with maximal morphological diversity. Such an assessment is unavoidably subjective, but this should not detract from its repeatability, provided the methods for assessment are explicitly outlined.

A variety of methods may be used to assess maximal morphological diversity, depending on the sources of information available for the terminal group. In studies addressing the relationships of higher taxa (e.g., orders and families), sampling for maximal morphological diversity may be analogous to sampling for maximum cladistic diversity (Wheeler et al., 1993) or adopting a divergent lineage strategy (Yeates, 1995). In these cases, a hierarchical classification exists for the terminal group, and exemplar species should be selected to represent the proposed groupings (i.e., families for ordinal studies, genera for familial studies) because they constitute current estimates of morphological diversity.

For studies intending to address the relationships of lower taxa (e.g., genera), such a hierarchical classification is usually absent, and additional criteria may be required for exemplar selection. Sampling for maximal morphological diversity therefore becomes more expansive than the maximum cladistic diversity or divergent lineage approaches, because divergence must be assessed without recourse to prior estimates of relationship. Biogeographical criteria, such as geographical disjunction, may be used in such cases, given that divergence may be correlated with disjunction. Phenetic assessments of divergence may need to be invoked in the absence of such information. Problem taxa, which have been debated in the taxonomic literature, or the phylogenetic positions of which have been speculated about (often on account of morphological divergence), should also be included as exemplars, to provide a test of these hypotheses.

Choice of maximally diverse taxa is a conservative strategy because it is designed to find interspecific character variation in the supraspecific taxon that could potentially falsify the hypothesis of monophyly. For example, a test of insect monophyly would be better achieved by including *Drosophila* and a basal apterygote than by including 2, or even 10, holometabolans (Wheeler et al., 1993). However, in the absence of prior knowledge of cladistic relationships, this method will not include a basal lineage unless the lineage happens to be divergent; indeed, there is no reason to expect that the method will sample any basal lineages at all (Yeates, 1995). Although this may appear to be a drawback, the alternative (random selection) is unlikely to perform better at sampling basal lineages and has the added disadvantage of potentially selecting sister species as exemplars, thereby providing a relatively weak test of the monophyly of the higher taxon.

Multiple Exemplars

The poor performance of sampling a single (randomly chosen) exemplar species from each higher taxon, relative to sampling all or even a few species, has been demonstrated (Wheeler, 1992; Wiens, 1998a). A minimum sample of two exemplars is necessary to distinguish character states that are autapomorphic or homoplasious from those that are synapomorphic for the higher taxon the exemplars represent (Wheeler et al., 1993).

Character states shared by exemplars constitute a parsimonious estimate of the groundplan for the higher taxon, an estimate that can be improved by including progressively more divergent exemplars. Accordingly, including more than two exemplars is desirable for representing diverse groups, in which interspecific variation is prevalent (e.g., Cantino, 1992).

Nomenclatural Exemplars

When hypotheses of monophyly and the internal cladistic structure of terminal groups are doubtful or unavailable, including the type taxon as an exemplar is advisable (Walker et al., 1990; Cantino, 1992; Yeates, 1995). For example, type species should be included as exemplars in analyses intending to test generic monophyly. This provides the possibility to determine which species form a monophyletic group with regard to the type species and which do not, thereby allowing the appropriate nomenclature to be ascertained for the resulting clades (Yeates, 1995).

Practical Exemplars

Despite these recommendations, the practical choice of exemplars for morphological studies is more commonly dictated by the availability of specimens for examination (which is most acute when taxa are known only from the holotype), just as the choice of exemplars for molecular studies is more commonly dictated by the availability of samples for DNA extraction (Bininda-Emonds et al., 1998). Where anatomical or behavioral data are concerned, exemplar selection may be dictated by which taxa have been most extensively studied. Selecting exemplars on the basis of such reasons could potentially bias results because critical character combinations may not appear in those taxa (Hormiga et al., 1995). However, the inclusion of relatively unstudied taxa could also increase the number of missing entries and hence the instability and ambiguity of the results (Nixon and Davis, 1991; Platnick et al., 1991).

These issues do not arise when supraspecific terminal taxa are used, because observations from different lower taxa can be combined in a single terminal. For example, Nixon and Carpenter (1996) advocate the fusion of terminal taxa in cases of data disjunction, when terminals do not share real observations for characters and hence there is no information relevant to their grouping. This is evidently an advantage of using supraspecific terminals, because the number of missing entries is minimized (and is the reason for using species, rather than individuals, as terminal taxa in exemplar analyses based on morphological data). However, this apparent advantage may be offset by the problem of coding interspecific variation (Wiens, 1998a). Possible solutions to the problem in exemplar analyses include the omission of taxa that introduce missing data in favor of others that do not, or in the case of well-known groups, explicit extrapolation from taxa for which these data are available (e.g., Muona, 1995).

CONCLUSIONS

Phylogenetic analyses will always be constrained by the practical availability of data. Operating within those constraints, I advocate the following strategy for exemplar choice:

1. A minimum of two exemplar species per higher taxon (unless monotypic) should be included in all analyses.
2. Type taxa should be included wherever possible, especially when monophyly is contested.
3. When hypotheses of relationships within terminal groups are available, an exemplar with a short branch length should be selected from each of the two branches arising from the root node.
4. When such hypotheses are unavailable, exemplars should be selected so as to maximize morphological diversity for the supraspecific taxa they will represent. The number of exemplars included in the analysis will then depend on a case-specific assessment of the interspecific variation

within each supraspecific taxon represented, such that more exemplars will be required to represent supraspecific taxa having greater variation (e.g., Cantino, 1992).

As with other scientific methods, the exemplar approach will not guarantee success. Nevertheless, as argued by Yeates (1995:354), "its chief advantage is that it facilitates future analyses, all assumptions being transparent," an advantage that will become increasingly important as morphological and molecular data are routinely integrated in simultaneous analyses of little-known groups and lower taxonomic levels.

ACKNOWLEDGMENTS

This research was supported by a Prestigious Scholarship from the Foundation for Research Development, Pretoria; the S.A. College Croll and Myer Levinson (EMDIN) Funds of the University of Cape Town; two Grants in Support of Research from the Theodore Roosevelt Memorial Fund of the American Museum of Natural History; a Collections Study Grant from the American Museum of Natural History; and an Ernst Mayr Grant from the Museum of Comparative Zoology, Harvard University. Additional support was provided by the American Arachnological Society, the California Academy of Sciences, and the Skye Foundation and Charitable Trust. These ideas were presented at the XIV International Congress of Arachnology and 22nd Annual Meeting of the American Arachnological Society, Chicago, 1998 (attendance supported by the American Arachnological Society), and at the Inaugural Conference of the South African Society for Systematic Biology, Stellenbosch, 1999. The development of this manuscript benefited from comments provided by the following individuals: James Carpenter, Jonathan Coddington, Timothy Crowe, Gonzalo Giribet, Charles Griswold, H. Peter Linder, Richard Olmstead, Norman Platnick, Ward Wheeler, and an anonymous reviewer. This acknowledgment should not be taken as their endorsement of any views expressed herein.

REFERENCES

ADACHI, J., AND M. HASEGAWA. 1995. Phylogeny of whales: Dependence of inference on species sampling. Mol. Biol. Evol. 12:177–179.

BEARD, K. C. 1993. Phylogenetic systematics of the Primatomorpha, with special reference to Dermoptera. Pages 129–150 *in* Mammal phylogeny, placentals (F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds.). Springer-Verlag, New York.

BININDA-EMONDS, O. R. P., H. N. BRYANT, AND A. P. RUSSELL. 1998. Supraspecific taxa as terminals in cladistic analysis: Implicit assumptions of monophyly and a comparison of methods. Biol. J. Linn. Soc. 64:101–133.

BININDA-EMONDS, O. R. P., AND A. P. RUSSELL. 1993. A morphological perspective on the phylogenetic relationships of the extant phocid seals (Mammalia: Carnivora: Phocidae). Bonn Zool. Monogr. 41:1–256.

BOGDANOWICZ, W., S. KASPER, AND R. D. OWEN. 1998. Phylogeny of plecotine bats. Reevaluation of morphological and chromosomal data. J. Mamm. 79:78–90.

BROTHERS, D. J., AND J. M. CARPENTER. 1993. Phylogeny of Aculeata: Chrysidoidea and Vespoidea (Hymenoptera). J. Hymenop. Res. 2:227–304.

BRYANT, H. N. 1997. Hypothetical ancestors and rooting in cladistic analysis. Cladistics 13:337–348.

BRYANT, H. N., A. P. RUSSELL, AND W. D. FITCH. 1993. Phylogenetic relationships within the extant Mustelidae (Carnivora): Appraisal of the cladistic status of the Simpsonian subfamilies. Zool. J. Linn. Soc. 108:301–334.

CANTINO, P. D. 1992. Evidence for a polyphyletic origin of the Labiatae. Ann. Mo. Bot. Gard. 79:361–379.

CHRISTOFFERSON, M. L. 1989. Phylogeny and classification of the Pandaloidea (Crustacea, Caridea). Cladistics 5:259–274.

CLARK, C., AND D. J. CURRAN. 1986. Outgroup analysis, homoplasy, and global parsimony: A response to Maddison, Donoghue and Maddison. Syst. Zool. 35:422–426.

COLLESS, D. H. 1985. On the status of outgroups in phylogenetics. Syst. Zool. 34:364–366.

CRACRAFT, J. 1983. Species concepts and speciation analysis. Curr. Ornithol. 1:159–187.

CRACRAFT, J. 1989. Speciation and its ontology: The empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. Pages 28–59 *in* Speciation and its consequences (D. Otte and J. A. Endler, eds.). Sinauer Associates, Sunderland, Massachusetts.

DAVIS, J. I., AND K. C. NIXON. 1992. Populations, genetic variation, and the delimitation of phylogenetic species. Syst. Biol. 41:421–435.

DE QUEIROZ, K. 1987. Phylogenetic systematics of iguanine lizards: A comparative osteological study. Univ. Calif. Publ. Zool. 118:1–203.

DONOGHUE, M. J. 1994. Progress and prospects in reconstructing plant phylogeny. Ann. Mo. Bot. Gard. 81:405–418.

DONOGHUE, M. J., AND J. A. DOYLE. 1989. Phylogenetic analysis of angiosperms and the relationships of Hamamelidae. Pages 17–45 *in* Evolution, systematics and fossil history of the Hamamelidae 1. Systematics Association special volume 40A (P. R. Crane and S. Blackmore, eds.). Clarendon Press, Oxford.

DONOGHUE, M. J., J. A. DOYLE, J. A. GAUTHIER, A. G. KLUGE, AND T. ROWE. 1989. The importance of fossils in phylogeny reconstruction. Annu. Rev. Ecol. Syst. 20:431–460.

DOYLE, J. A., M. J. DONOGHUE, AND E. A. ZIMMER. 1994. Integration of morphological and ribosomal RNA data on the origin of angiosperms. Ann. Mo. Bot. Gard. 81:419–450.

DRAGOO, J. W., AND R. L. HONEYCUTT. 1997. Systematics of mustelid-like carnivores. J. Mammal. 78:426–443.

EERNISSE, D. J., AND A. G. KLUGE. 1993. Taxonomic congruence versus total evidence, and amniote phylogeny inferred from fossils, molecules, and morphology. Mol. Biol. Evol. 10:1170–1195.

Estes, R., K. de Queiroz, and J. A. Gauthier. 1988. Phylogenetic relationships within Squamata. Pages 119–281 *in* Phylogenetic relationships of the lizard families (R. Estes and G. K. Pregill, eds.). Stanford Univ. Press, Stanford, California.

Farris, J. S. 1983. The logical basis of phylogenetic analysis. Pages 7–36 *in* Advances in cladistics, volume 2 (N. I. Platnick and V. A. Funk, eds.). Columbia Univ. Press, New York.

Felsenstein, J. 1978. The number of evolutionary trees. Syst. Zool. 27:27–33.

Frost, D. R., and A. G. Kluge. 1994. A consideration of epistemology in systematic biology, with special reference to species. Cladistics 10:259–294.

Goloboff, P. A. 1993. A reanalysis of mygalomorph spider families (Araneae). Am. Mus. Novit. 3056:1–32.

Graybeal, A. 1998. Is it better to add taxa or characters to a difficult phylogenetic problem? Syst. Biol. 47: 9–17.

Grimaldi, D. A. 1990. A phylogenetic, revised classification of the genera in the Drosophilidae (Diptera). Bull. Am. Mus. Nat. Hist. 197:1–139.

Griswold, C. E., J. A. Coddington, G. Hormiga, and N. Scharff. 1998. Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea). Zool. J. Linn. Soc. 123:1–99.

Halanych, K. M. 1998. Lagomorphs displaced by more characters and fewer taxa. Syst. Biol. 47:138–146.

Hausdorf, B. 1995. A preliminary phylogenetic and biogeographic analysis of the Dyakiidae (Gastropoda: Stylommatophora) and a biogeographic analysis of other Sundaland taxa. Cladistics 11:359–376.

Hendy, M. D., and D. Penny. 1989. A framework for the quantitative study of evolutionary trees. Syst. Zool. 38:297–309.

Hillis, D. M. 1996. Inferring complex phylogenies. Nature 383:130–131.

Hormiga, G., W. G. Eberhard, and J. A. Coddington. 1995. Web-construction behaviour in Australian *Phonognatha* and the phylogeny of nephiline and tetragnathid spiders (Araneae: Tetragnathidae). Aust. J. Zool. 43:313–364.

Judd, D. D. 1996. Review of the systematics and phylogenetic relationships of the Sabethini (Diptera: Culicidae). Syst. Entomol. 21:129–150.

Kim, J. 1996. General inconsistency conditions for maximum parsimony: Effects of branch lengths and increasing numbers of taxa. Syst. Biol. 45:363–374.

Kluge, A. G. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). Syst. Zool. 38:7–25.

Kluge, A. G. 1997. Testability and the refutation and corroboration of cladistic hypotheses. Cladistics 13:81–96.

Kron, K. A., and W. S. Judd. 1997. Systematics of the *Lyonia* Group (Andromedeae, Ericaceae) and the use of species as terminals in higher-level cladistic analyses. Syst. Bot. 22:479–492.

Lecointre, G., H. Philippe, H. L. Vân Lê, and H. Le Guyader. 1993. Species sampling has a major impact on phylogenetic inference. Mol. Phylogenet. Evol. 2:205–224.

Livezey, B. C. 1986. A phylogenetic analysis of recent anseriform genera using morphological characters. Auk 103:737–754.

Livezey, B. C. 1996. A phylogenetic reassessment of the tadornine–anatine divergence (Aves: Anseriformes: Anatidae). Ann. Carnegie Mus. 65:27–88.

Marvaldi, A. E. 1997. Higher-level phylogeny of the Curculionidae (Coleoptera, Curculionoidea) based mainly on larval characters, with special reference to broad-nosed weevils. Cladistics 13:285–312.

Meacham, C. A. 1984. The role of hypothesized direction of characters in the estimation of evolutionary history. Taxon 33:26–38.

Meacham, C. A. 1986. More about directed characters: A reply to Donoghue and Maddison. Taxon 35:538–540.

Meier, R. 1997. A test and review of the empirical performance of the ontogenetic criterion. Syst. Biol. 46:699–721.

Miller, J. S. 1991. Cladistics and classification of the Notodontidae (Lepidoptera: Noctuoidea) based on larval and adult morphology. Bull. Am. Mus. Nat. Hist. 204:1–230.

Miller, J. S., A. V. Z. Brower, and R. DeSalle. 1997. Phylogeny of the Neotropical moth tribe Josiini (Notodontidae, Dioptinae): Comparing and combining evidence from DNA-sequences and morphology. Biol. J. Linn. Soc. 60:297–316.

Mishler, B. D. 1994. Cladistic analysis of molecular and morphological data. Am. J. Phys. Anthropol. 94:143–156.

Morrone, J. J. 1997. Cladistics of the New World genera of Listroderina (Coleoptera: Curculionidae: Rhytirrhinini). Cladistics 13:247–266.

Muona, J. 1995. The phylogeny of Elateroidea (Coleoptera), or which tree is best today? Cladistics 11:317–341.

Nandi, W. I., M. W. Chase, and P. K. Endress. 1998. A combined cladistic analysis of angiosperms using *rbc*L and non-molecular data sets. Ann. Mo. Bot. Gard. 85:137–212.

Nelson, G., and N. I. Platnick. 1981. Systematics and biogeography: Cladistics and vicariance. Columbia Univ. Press, New York.

Nielsen, E. S., and N. P. Kristensen. 1996. The Australian moth family Lophocoronidae and the basal phylogeny of the Lepidoptera-Glossata. Invert. Taxon. 10:1199–1302.

Nixon, K. C., and J. M. Carpenter. 1993. On outgroups. Cladistics 9:413–426.

Nixon, K. C., and J. M. Carpenter. 1996. On simultaneous analysis. Cladistics 12:221–241.

Nixon, K. C., and J. I. Davis. 1991. Polymorphic taxa, missing values, and cladistic analyis. Cladistics 7:233–241.

Nixon, K. C., and Q. D. Wheeler. 1990. An amplification of the phylogenetic species concept. Cladistics 6:211–223.

Platnick, N. I., C. E. Griswold, and J. A. Coddington. 1991. On missing entries in cladistic analysis. Cladistics 7:337–343.

Poe, S., and D. L. Swofford. 1999. Taxon sampling revisited. Nature 398:299–300.

Polly, P. D. 1996. The skeleton of *Gazinocyon vulpeculus* gen. et comb. nov. and the cladistic relationships of Hyaenodontidae (Eutheria, Mammalia). J. Vert. Palaeontol. 16:303–319.

Raven, R. J. 1985. The spider infraorder Mygalomorphae (Araneae): Cladistics and systematics. Bull. Am. Mus. Nat. Hist. 182:1–180.

Rice, K. A., M. J. Donoghue, and R. G. Olmstead. 1997. Analyzing large data sets: *rbc*L 500 revisited. Syst. Biol. 46:554–563.

ROGNES, K. 1997. The Calliphoridae (blowflies) (Diptera: Oestridae) are not a monophyletic group. Cladistics 13:27–66.

ROSELL, D., AND M. J. URIZ. 1997. Phylogenetic relationships within the excavating Hadromerida (Porifera), with a systematic revision. Cladistics 13:349–366.

SHAFFER, H. B., P. MEYLAN, AND M. L. MCKNIGHT. 1997. Tests of turtle phylogeny: Molecular, morphological and palaeontological approaches. Syst. Biol. 46:235–268.

SHULTZ, J. W. 1990. Evolutionary morphology and phylogeny of Arachnida. Cladistics 6:1–38.

SMITH, J. F. 1996. Tribal relationships within Gesneriaceae: A cladistic analysis of morphological data. Syst. Bot. 21:497–513.

SOLTIS, D. E., P. S. SOLTIS, M. E. MORT, M. W. CHASE, V. SAVOLAINEN, S. B. HOOT, AND C. M. MORTON. 1998. Inferring complex phylogenies using parsimony: An empirical approach using three large DNA data sets for angiosperms. Syst. Biol. 47:32–42.

TRUEB, L., AND R. CLOUTIER. 1991. A phylogenetic investigation of the inter- and intrarelationships of the Lissamphibia (Amphibia: Temnospondyli). Pages 223–313 *in* Origins of the higher groups of tetrapods: Controversy and consensus. (H.-P. Schultze and L. Treub, eds.). Cornell Univ. Press, Ithaca, New York.

VRANA, P., AND W. C. WHEELER. 1992. Individual organisms as terminal entities: Laying the species problem to rest. Cladistics 8:67–72.

WALKER, A. K., I. J. KITCHING, AND A. D. AUSTIN. 1990. A reassessment of the phylogenetic relationships within the Microgastrinae (Hymenoptera: Braconidae). Cladistics 6:291–306.

WHEELER, Q. D., AND K. C. NIXON. 1990. Another way of *looking at* the species problem: A reply to de Queiroz and Donoghue. Cladistics 6:77–81.

WHEELER, W. C. 1992. Extinction, sampling, and molecular phylogenetics. Pages 205–215 *in* Extinction and phylogeny (M. Novacek and Q. Wheeler, eds.). Columbia Univ. Press, New York.

WHEELER, W. C., P. CARTWRIGHT, AND C. HAYASHI. 1993. Arthropod phylogeny: A combined approach. Cladistics 9:1–39.

WHEELER, W. C., AND C. Y. HAYASHI. 1998. The phylogeny of extant chelicerate orders. Cladistics 14:173–192.

WHITING, M. F., J. M. CARPENTER, Q. D. WHEELER, AND W. C. WHEELER. 1997. The Strepsiptera problem: Phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA sequences and morphology. Syst. Biol. 46:1–68.

WIENS, J. J. 1998a. The accuracy of methods for coding and sampling higher-level taxa for phylogenetic analysis: A simulation study. Syst. Biol. 47:397–413.

WIENS, J. J. 1998b. Testing phylogenetic methods with tree congruence: Phylogenetic analysis of polymorphic morphological characters in Phrynosomatid lizards. Syst. Biol. 47:427–444.

WILEY, E. O., G. D. JOHNSON, AND W. W. DIMMICK. 1998. The phylogenetic relationships of Lampridiform fishes (Teleostei, Acanthomorpha), based on a total-evidence analysis of morphological and molecular data. Mol. Phylogenet. Evol. 10:417–425.

YEATES, D. K. 1994. The cladistics and classification of the Bombyliidae (Diptera: Asiloidea). Bull. Am. Mus. Nat. Hist. 219:1–191.

YEATES, D. K. 1995. Groundplans and exemplars: Paths to the tree of life. Cladistics 11:343–357.

ZRZAVÝ, J., S. MIHULKA, P. KEPKA, A. BEZDEK, AND D. TIETZ. 1998. Phylogeny of the Metazoa based on morphological and 18S ribosomal DNA evidence. Cladistics 14:249–285.